

Abundance of giant sea anemones and patterns of association with anemonefish in the northern Red Sea

Nanette E. Chadwick*‡ and Michael Arvedlund†

*Faculty of Life Sciences, Bar Ilan University, Ramat Gan 52900, Israel, and Interuniversity Institute for Marine Science, Eilat 88103, Israel. †University of the Ryukyus, Tropical Biosphere Research Center, Sesoko Station, Sesoko 3422, Motobu, Okinawa 905-0227, Japan. ‡Present address of corresponding author: Department of Biological Sciences, 101 Rouse Life Sciences Building, Auburn University, Auburn, AL 36849-5407, USA. E-mail: chadwick@auburn.edu

Patterns of distribution and abundance of giant sea anemones and anemonefish were compared among coral reefs along the coastline of Sinai in the northern Red Sea. The sea anemones varied widely in abundance between reef areas containing different habitat types. They were rare on steep reef slopes with abundant coral cover (=low-density anemone sites, 0.09–0.68 anemones per 1000 m² of reef area), but were common at a site containing patch reefs interspersed with sand (=high-density anemone site, 6.00–8.11 anemones per 1000 m²). Distributions of the endemic two-band anemonefish (*Amphiprion bicinctus*) varied significantly between the two main host anemone species. At the high-density site, individuals of the sea anemone *Heteractis crispa* either did not contain anemonefish, or were occupied by single juvenile fish as shown in previous studies. At low-density sites *H. crispa* usually hosted clusters of juvenile anemonefish. In contrast, individuals of the sea anemone *Entacmaea quadricolor* hosted either single adult fish (high-density site) or pairs of breeding adults (low-density sites), frequently in addition to some juvenile fish. Mechanisms that prevent anemonefish from reaching adult size and forming breeding pairs in *H. crispa* may include high fish mortality above a size threshold because this host cannot adequately protect them from predation when they become large, active emigration of fish to *E. quadricolor* as described in previous reports, and/or environmentally-controlled cessation of fish growth. We conclude that in the northern Red Sea, individuals of *H. crispa* potentially serve as nurseries for anemonefish.

INTRODUCTION

Anemonefish and their associated giant sea anemones are conspicuous components of coral reefs throughout much of the tropical Indo-Pacific region (Fautin & Allen, 1997). Individuals of the ten known species of host sea anemones are ecologically important members of reef communities, in that they provide habitat for 28 species of fish and numerous shrimps, many of which are obligate symbionts (Bruce & Svoboda, 1983; Fautin, 1991). Some shrimps that associate with anemones serve as cleaners of parasites from larger reef fish (Sargent & Wagenbach, 1975), thus the importance of this symbiosis extends beyond the anemones and their symbionts.

Species-specific patterns of association between host anemones and anemonefish have been documented (Fautin, 1986, 1991; Elliot et al., 1995; Elliot & Mariscal, 2001), but no quantitative data are available on fish size distributions among sympatric anemone species. Several authors have described qualitative patterns of juvenile versus adult anemonefish distribution among host anemone species (Fishelson, 1965, 1970; Fricke, 1974; Fautin & Allen, 1997; Maroz & Fishelson, 1997). However, the number of anemones that host anemonefish of different size-classes is not known for any assemblage of co-occurring sea anemone species.

Some anemones may serve as nurseries for anemonefish in that they host mainly juveniles (Fishelson, 1965; Fautin

& Allen, 1997). A nursery habitat for fish is one that contributes a large proportion of individuals to the adult population relative to other habitats in which juveniles occur (Beck et al., 2001). In the northern Red Sea, the endemic anemonefish *Amphiprion bicinctus* inhabits three anemone species: *Entacmaea quadricolor* (= *Gyrostoma* sp.), *Heteractis crispa* (= *Radianthus koseirensis*), and *H. magnifica* (Fishelson, 1970; Fricke, 1974; Fautin & Allen, 1997). Individuals of *H. magnifica* are rare, but when present they may host fish of all sizes in large aggregations such as at ‘anemone city’ in the southern Sinai (Brolund et al., 2004). In contrast, individuals of the anemone *H. crispa* host juvenile fish (*A. bicinctus*), while individuals of *E. quadricolor* contain both juveniles and adults (Fishelson, 1970; Fricke, 1974). Thus, individuals of *H. crispa* appear to serve as nurseries for these anemonefish. Determination of nursery habitats for reef fish is important in understanding their movement patterns and population dynamics, and as a tool for the conservation management of populations (Adams & Ebersole, 2002; Nagelkerken et al., 2002). In addition, quantification of nursery patterns in Red Sea anemonefish can be used to inform repopulation experiments as part of restoration programmes for impoverished anemonefish populations (Maroz & Fishelson, 1997).

We quantify here patterns of abundance and size of the most common host sea anemones and anemonefish at reef sites in the northern Red Sea, and discuss possible roles of the anemones as nursery versus adult habitat for the fish.

MATERIALS AND METHODS

Surveys of anemonefish and host sea anemones were conducted at ten haphazardly-selected sites along the western shore of the Gulf of Aqaba and at the southern tip of the Sinai Peninsula in the northern Red Sea (Figure 1) during 12 May–24 July 2002. At the nine southernmost sites, the habitat type examined was narrow fringing reef with a steep slope that dropped vertically to a depth of 30–60 m, as described by Mergner (1971). At the northernmost site located adjacent to the Interuniversity Institute for Marine Science (Steinitz Marine Laboratory) near Eilat, the habitat type examined was patch reefs interspersed with beach rock, rubble and sand on a gradual slope to 12 m depth, followed by a steep rubble slope to at least 40 m depth, as described by Dafni & Tobol (1986) as site A, and by Vago et al. (1998) as site two. At each site, we surveyed an area extending for 300 m along the shore and 30 m down the reef slope ($300 \times 30 \text{ m} = 9000 \text{ m}^2$ per site). This area encompassed about 0–25 m depth on the steep slopes of the nine southern sites, and 0–15 m depth on the more gradual slope of the northern site at Eilat. At each site, SCUBA divers swam along depth clines and searched reef crevices and holes in order to locate all giant sea anemones (*Entacmaea quadricolor*, *Heteractis crispa*, *H. magnifica*) occurring within the survey area. The following information was collected for each anemone and anemonefish encountered: anemone species and size (diameter of tentacle crown=distance from tentacle tip to tentacle tip when fully expanded, after Porat & Chadwick-Furman, 2004), anemonefish species, number and size (total length of each fish in cm), and depth below sea surface. Host anemones and anemonefish were identified according to Fautin & Allen (1997). Anemones that appeared contracted (=tentacles and oral disk not fully expanded, Porat & Chadwick-Furman, 2004) during initial

examination were marked with a plastic flag and revisited until observed to fully expand, and tentacle crown diameter then was measured. *Amphiprion bicinctus* fish were classified as juveniles (0.5–6.0 cm) or adults (>6.0 cm). We use the term juvenile in the sense of Balon (1999) in that indirectly-developing fish, such as *A. bicinctus*, have a distinct larval period that ends in metamorphosis, from which the fish emerge as juveniles. Larval anemonefish metamorphose and recruit to anemones at about 0.5–1.0 cm total length (Ochi, 1986; Hattori, 1991); individuals smaller than about 0.5 cm were not encountered in the anemones (M. Arvedlund, personal observation). Size at sexual maturity of anemonefish is known to be under social control, but in *A. bicinctus* the minimum size for development of gonads is 6 cm total length in the Red Sea (Fricke, 1983) or larger for members of other *Amphiprion* species (Ochi, 1986; Hattori, 1991). Because of this, 6 cm total length was selected as a minimum adult size. Thus, our estimates of adult fish abundance represent maximal numbers, and may include some fish not yet sexually mature. Data are presented as means \pm standard deviation unless otherwise indicated.

RESULTS

Giant anemones were rare at the nine southern sites that contained steep reef slopes, so data from these sites were combined and analysed as a group. We observed 47 individuals of *Entacmaea quadricolor* at these sites combined, resulting in an abundance of 6.11 ± 2.33 individuals per site (range=3–10) or 0.68 ± 0.25 per 1000 m^2 of reef area ($N=9$ sites). Only eight individuals of *Heteractis crispa* were observed at all southern sites combined, resulting in an abundance of 0.88 ± 0.74 individuals per site (range=0–2) or 0.09 ± 0.08 per 1000 m^2 ($N=9$ sites). In the northern Red Sea, individuals of *Heteractis magnifica* are rare, and were observed only near an area termed ‘anemone city’ at Ras Mohammed and a few kilometres further north at Ras Ghazlani (Brolund et al., 2004; Figure 1).

At the northern site with patch reefs (Figure 1), members of the first two anemone species were common. We recorded 54 individuals of *E. quadricolor* at this site, at an abundance of 6.00 per 1000 m^2 (about $10 \times$ their

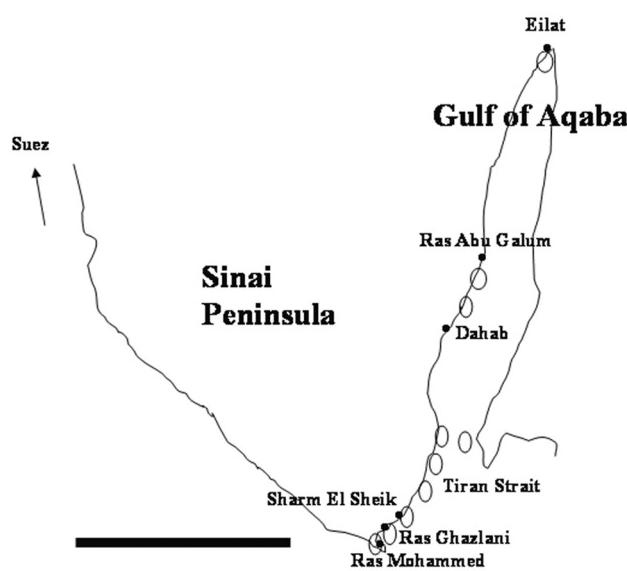


Figure 1. Map of ten study sites in the Gulf of Aqaba and northern Red Sea. The location of each site is indicated by an oval. Note that there are nine sites along the mid to southern Sinai Peninsula, and one site at the northern tip (Eilat). Scale bar: 100 km.

Table 1. Depth distribution of two species of giant sea anemones at study sites in the Gulf of Aqaba and northern Red Sea.

Depth (m)	Number of <i>Entacmaea quadricolor</i>		Number of <i>Heteractis crispa</i>	
	N	S	N	S
0–5	27	13	43	4
6–10	20	12	23	3
11–15	7	9	7	0
16–20	n.d.	10	n.d.	1
21–25	n.d.	3	n.d.	0
All depths	54	47	73	8

N, northern site at Eilat; S, southern sites along the Sinai Peninsula; n.d., no data.

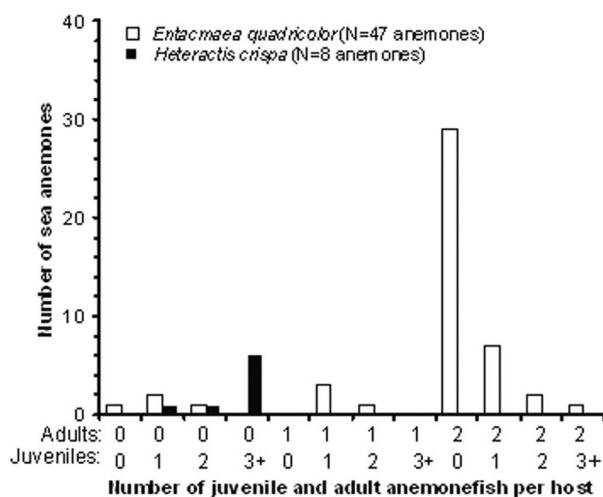
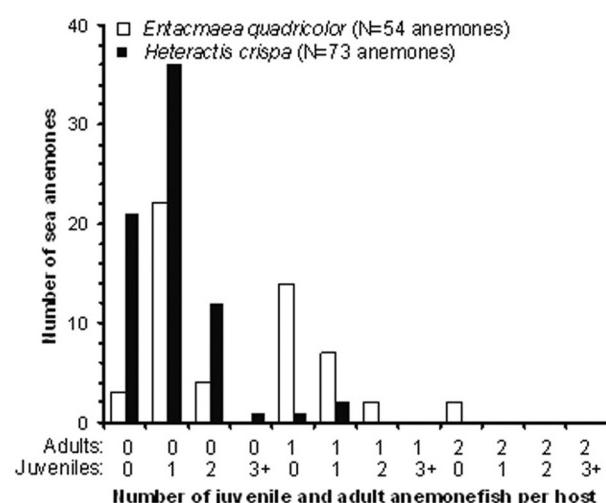
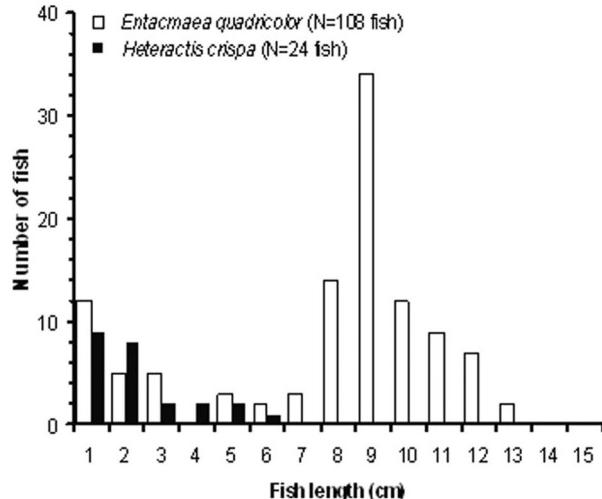
A**A****B**

Figure 2. Patterns of anemonefish (*Amphiprion bicinctus*) association with giant sea anemones (*Entacmaea quadricolor* and *Heteractis crispa*) at southern reef sites along the Sinai Peninsula, northern Red Sea. Due to small numbers of anemones at each site, data were pooled for all nine southern sites examined. (A) Number of juvenile and adult anemonefish per sea anemone host. The four sets of 0, 1, and 2 adults represent different combinations with juvenile fish in host anemones; (B) size distributions of anemonefish in giant sea anemones.

abundance on southern reefs), and 73 individuals of *H. crispa* at an abundance of 8.11 per 1000 m² (about 100× their abundance on reefs in the south).

Anemone abundance decreased with depth at 0–15 m for both species at both types of sites (Table 1). Abundance also was low at 16–25 m depth where it was examined on reef slopes at the southern sites (Table 1).

Individuals of *E. quadricolor* were significantly larger at low-density sites in the south (anemone diameter = 30.1 ± 12.3 cm, range = 10–48 cm, N = 47 individuals) than at the high-density site at the northern tip of the gulf (anemone diameter = 17.1 ± 7.4 cm diameter, range = 6–40 cm, N = 54 individuals, t-test, $t = -6.49$, $P < 0.001$). In contrast, the size of individuals of *H. crispa* did not differ significantly between low-density southern sites

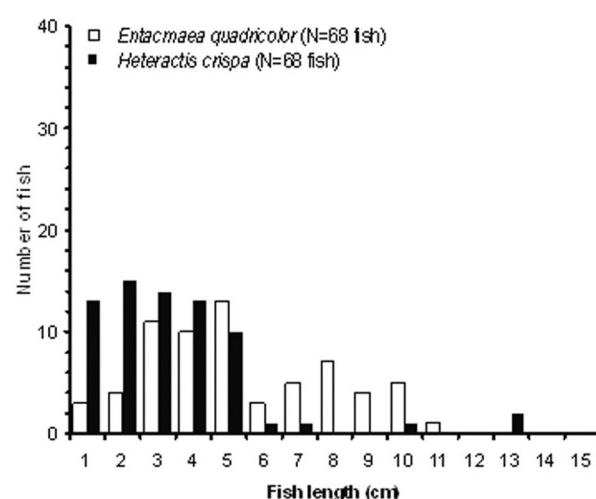
B

Figure 3. Patterns of anemonefish (*Amphiprion bicinctus*) association with giant sea anemones (*Entacmaea quadricolor* and *Heteractis crispa*) at a reef site near Eilat, northern tip of the Gulf of Aqaba, Red Sea. Due to large numbers of sea anemones at this site, it was analysed separately from southern sites. (A) Number of juvenile and adult anemonefish per sea anemone host. The four sets of 0, 1, and 2 adults represent different combinations with juvenile fish in host anemones; (B) size distributions of anemonefish in giant sea anemones.

(anemone diameter = 19.9 ± 11.7 cm, range = 10–41 cm, N = 8 individuals) and the high-density northern site (anemone diameter = 19.7 ± 6.4 cm diameter, range = 3–28 cm, N = 73 individuals, t-test, $t = 0.01$, $P = 0.55$). When comparing the two host species at all sites, individuals of *E. quadricolor* were not significantly larger than those of *H. crispa* (t-test, $t = 0.044$, $P = 0.90$); host anemones were on average about 20–30 cm in diameter.

As expected and based on the host distributional patterns, individuals of the anemonefish *Amphiprion bicinctus* also were ~10× more common at the high-density site near Eilat than they were on low-density reefs in the south (136 vs 14.67 anemonefish per site and 15.11 vs 1.63 per 1000 m² of reef area, respectively).

At the southern sites, most individuals of *E. quadricolor* contained two adult fish (83.0%, N=47 anemones, adult fish defined as >6.0 cm total length, see Materials and Methods), 8.5% had only one adult fish, and 8.5% contained no adults (Figure 2A). Some *E. quadricolor* anemones also harboured one or two juvenile fish, rarely three (Figure 2A). The size distribution of fish in *E. quadricolor* revealed that most fish were adults (6–13 cm total length), while some were very small juveniles of only 1–3 cm length (Figure 2B). Individuals of *E. quadricolor* at southern sites harboured 2.32 ± 1.07 fish per anemone (N=47 anemones). In contrast, most individuals of *H. crispa* at southern sites contained three or more very small juvenile fish (Figure 2), so there were 3.00 ± 1.12 fish per anemone of this species at southern sites (N=8 anemones).

At the northern site, only two individuals of *E. quadricolor* each harboured a pair of adult fish (5.7%, N=54 anemones), 42.6% each contained a single adult fish, and more than half of the anemones of this species (53.7%) had no adults at all (Figure 3A). Of the anemones that contained no adult fish, most harboured juveniles, so that few specimens of *E. quadricolor* at this site lacked fish completely (Figure 3A). The population of anemonefish inhabiting individuals of *E. quadricolor* at Eilat lacked newly-settled juveniles (1–2 cm total length, Figure 3A). No individuals of the sea anemone *H. crispa* harboured sexually mature pairs of fish at Eilat, as described previously by Fishelson (1965, 1970). A few contained single adult fish (4.1%, N=73 anemones), but most harboured one or two juveniles (65.7%, Figure 3A). A substantial proportion of individuals of *H. crispa* at Eilat lacked fish completely (28.8%, Figure 3A). Of those occupied by fish, individuals of *H. crispa* at Eilat contained a relatively even distribution of juvenile size-classes (Figure 3B), whereas members of both anemone species were skewed toward smaller fish recruits at southern sites (Figure 2B).

DISCUSSION

The abundance of giant sea anemones and their anemonefish varied significantly among reef sites in the northern Red Sea. This pattern may be caused by factors related to reef latitude, but more likely depends on variation in reef habitat type among the sites examined. The northern site where anemones were most abundant consists of patch reefs interspersed with soft substrate, a habitat type known to be more favourable to giant anemones than are the densely coral-covered outer reef slopes (Fautin, 1988; Elliot & Mariscal, 2001) examined at the southern sites. The former habitat offers more reef holes and rubble for anemones to occupy, while crowded stony corals in the latter habitat may leave less space for anemones. Thus, less suitable anemone habitat may be available per square metre at reef sites examined in the south, compared to the disturbed rubble habitat with fewer live corals in Eilat. Fricke (1974) also observed high abundances of *Heteractis crispa* (=*Radianthus* sp.) and *Entacmaea quadricolor* (=*Gyrostoma* sp.) on coral reefs at Eilat. The extreme rarity of *H. crispa* at southern sites (see Results) may result in part from this anemone's preference for the reef–sand interface and even for habitats entirely surrounded by sand, since this anemone is a typical sand-dweller (Dunn, 1981; Chadwick & Arvedlund, personal

observation). In Papua New Guinea, individuals of *H. crispa* also are more abundant on nearshore and lagoonal areas of patch reefs and sand than on steep outer reef slopes (Elliot & Mariscal, 2001). At our study sites in the Red Sea, both anemone species were most abundant at shallow depths (Table 1), indicating that our surveys of shallow areas likely included most of the giant anemones present at each site.

The significantly smaller size of the sea anemone *E. quadricolor* at Eilat than at the southern sites may be due in part to their lack of breeding pairs of anemonefish. The growth rate and survival of individuals of *E. quadricolor* varies with the size and number of their resident anemonefish (Porat & Chadwick-Furman, 2004). In French Polynesia, anemonefish have been shown to augment the growth rate and body size of their host sea anemones (Holbrook & Schmitt, 2005). Thus, some anemones may be unable to maintain large body size because they do not harbour enough adult fish to receive adequate nutritional and other benefits (Porat & Chadwick-Furman, 2005).

Several mechanisms may cause the observed patterns of host occupancy by anemonefish in the Red Sea. Fish living in *H. crispa* may experience high mortality upon reaching a threshold size (possibly 5 cm total length, Figures 2B & 3B) because this host cannot adequately protect them from predation when they become large. Fish survival in *H. crispa* thus may be size-dependent, with most fish doomed to die once they become too large in this host. Thus, individuals of the anemonefish *Amphiprion bicinctus* may prefer to recruit to *E. quadricolor*, but if no other habitat is available, they will recruit to *H. crispa*, where they suffer high mortality. Alternately, as growth and sexual maturity are known to be under social control in anemonefish (Hattori, 1991; Buston, 2003), fish also may arrest their growth based on environmental cues received from the host anemone. Anemonefish *Amphiprion bicinctus* that occupy the sea anemone *H. crispa* in the Red Sea simply may stop growing upon reaching ~5 cm total length (Figures 2B & 3B), and remain small juveniles for the duration of their occupancy of this host anemone. Finally, at this same size threshold, fish may actively disperse and search for a new host, migrating to individuals of *E. quadricolor* where they are able to continue growing and to reach sexual maturity. These hypotheses are not mutually exclusive, and a combination of all three may be reflected in the population dynamics of these fish.

At the northern site, the anemone *H. crispa* harboured more juvenile fish than did *E. quadricolor* (Figure 3). Thus, they fit Beck et al.'s (2001) definition of a nursery habitat, if these juveniles recruit to the adult fish population. However, individuals of *H. crispa* may not serve in a strict sense as nurseries, since they did not occur at all sites (see Results), some of them harboured adult fish (Figure 3A), and some of the juvenile fish lived with the alternate host *E. quadricolor*. In the western Pacific, individuals of *H. crispa* may host adult pairs of some anemonefish species (Elliott & Mariscal, 2001, and references therein). In contrast, the congeneric anemones *H. aurora* and *H. malu* are known to host mainly juvenile anemonefish, and have been termed nursery anemones (Fautin & Allen, 1997). It appears that some members of this genus are suboptimal hosts for

certain anemonefish species, and lack traits that allow these fish to mature and reproduce.

Anemonefish move among host anemones if they are adjacent and not fully occupied (Ochi, 1986; Hattori, 1991; Elliot & Mariscal, 2001; Brolund et al., 2004). When experimentally displaced from host anemones at Eilat, adult anemonefish can return to the same host if <40–50 m distant (Fricke, 1974). In Papua New Guinea, anemonefish can swim at least 20 m to occupy new hosts (Elliot & Mariscal, 2001). The nearest neighbour distance between individuals of *E. quadricolor* and *H. crispa* at our high-density site was <10 m on average (N.E. Chadwick, unpublished data). Thus, anemones often were located close enough for anemonefish to move between them. If displaced <20–30 m from an anemone, adult fish *A. bicinctus* exhibit a distinctive back-and-forth swimming motion ('schaukelschwimmen') in which they search for their original host (Fricke, 1974). The same behaviour could be used when searching for a more optimal host upon active desertion of the original anemone. Settling and juvenile anemonefish can detect hosts chemically (reviewed in Brolund et al., 2003). Juvenile anemonefish have a well-developed olfactory system, encompassing both ciliated and microvillous olfactory receptors (Arvedlund et al., 2003). In addition, large juvenile *A. bicinctus* have been shown to use visual cues when recognizing host anemones (Fricke, 1974). Large juvenile *A. bicinctus* thus possess well-developed physiological and behavioural mechanisms for successful transfer between hosts if needed.

What characteristics of host anemone species cause their fish symbionts to vary in population structure? Anemone hosts provide physical protection from predation to their anemonefish (Fautin, 1991) and within species the number and size of fish may vary with host size (Richardson, 1999; Elliot & Mariscal, 2001). Anemonefish presence can also augment host anemone size, so size effects potentially are reciprocal between fish and host (Porat & Chadwick-Furman, 2004; Holbrook & Schmitt, 2005). At our sites in the Red Sea, size variation between host anemone species does not appear responsible for fish size differences, because this trait did not vary significantly between host species (see Results). However, individuals of *E. quadricolor* possess thick tentacles with rounded blunt tips, which may expand into spherical bulbs when stimulated by anemonefish (Fautin & Allen, 1997) and may offer more surface area for physical protection of anemonefish than do the thinner, pointed tentacles of *H. crispa*. Other traits that might possibly differ between these anemone species, such as composition of their chemical toxins, behavioural responses to attack by piscivores, or microhabitat distribution, also may contribute to differences in their fish populations. Both *H. crispa* and *E. quadricolor* are known to associate with a wider diversity of anemonefish species than do most other host anemone species (14 and 13 species respectively, Fautin & Allen, 1997), but *H. crispa* may be limited to sheltering mainly juveniles of some fish species.

We conclude that giant sea anemones vary in their abundance and in the size of their anemonefish occupants in the Red Sea, due in part to morphological and other traits of the hosts. Patterns of fish occupancy may develop through a combination of differential fish recruitment,

growth, mortality, and/or dispersal among host species. To determine definitively whether some giant anemones serve as nurseries for anemonefish, tagging studies are needed to track the movement patterns of juvenile fish from potential nursery anemones into the adult fish population.

We thank the New Waves Dive Club at Sharm El Sheik and the Interuniversity Institute for Marine Science at Eilat for technical support during the field work. PADI dive master A. Samir arranged for diving surveys at Ras Abu Galum, and A.J. de Grissard (Director, Nature Conservation and Management Centre at Sharm El Sheik) provided advice and permits to conduct research in Ras Mohammed National Park. T.M. Brolund and S. Ichida assisted with surveys at Sharm El Sheik, and K. Tarnaruder with surveys at Eilat. The manuscript was improved by comments from two anonymous referees. Financial support was provided by grants from the COWI-Foundation of Denmark to M.A. and from Bar Ilan University to N.E.C. This research complies with current laws in Israel and Egypt where the field observations were performed.

REFERENCES

- Adams, A.J. & Ebersole, J.P., 2002. Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series*, **228**, 213–226.
- Arvedlund, M., Brolund, T.M. & Nielsen, L.E., 2003. The morphology of the peripheral olfactory organ in the juvenile anemonefish *Amphiprion ocellaris* and *Dascyllus aruanus*. *Journal of the Marine Biological Association of the United Kingdom*, **83**, 1321–1326.
- Balon, E.K., 1999. Alternative ways to become a juvenile or a definitive phenotype (and some persisting linguistic offences). *Environmental Biology of Fishes*, **56**, 17–38.
- Beck, M.W. et al., 2001. The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience*, **51**, 633–641.
- Brolund, T.M., Nielsen, L.E. & Arvedlund, M., 2003. Do juvenile *Amphiprion ocellaris* (Pisces: Pomacentridae) recognize conspecifics by chemical or visual cues? *Journal of the Marine Biological Association of the United Kingdom*, **83**, 1127–1136.
- Brolund, T.M., Tychsen, A., Nielsen, L.E. & Arvedlund, M., 2004. An assemblage of the host anemone *Heteractis magnifica* in the northern Red Sea, and distribution of the resident anemonefish. *Journal of the Marine Biological Association of the United Kingdom*, **84**, 671–674.
- Bruce, A.J. & Svoboda, A., 1983. Observations upon some pontoniine shrimps from Aqaba, Jordan. *Zoologische Verhandelingen*, **205**, 3–44.
- Buston, P., 2003. Size and growth modification in clownfish. *Nature, London*, **424**, 145–146.
- Dafni, J. & Tobol, R., 1986. Population structure patterns of a common Red Sea echinoid (*Tripneustes gratilla elatensis*). *Israel Journal of Zoology*, **34**, 191–204.
- Dunn, D.F., 1981. The clownfish sea anemones. Stichodactylidae (Coelenterata: Actiniaria) and other sea anemones symbiotic with pomacentrid fishes. *Transactions of the American Philosophical Society*, **71**, 1–115.
- Elliot, J.K., Elliot, J.M. & Mariscal, R.N., 1995. Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Marine Biology*, **122**, 377–389.
- Elliot, J.K. & Mariscal, R.N., 2001. Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. *Marine Biology*, **138**, 23–36.
- Fautin, D.G., 1986. Why do anemonefishes inhabit only some host actinians? *Environmental Biology of Fishes*, **15**, 171–180.

- Fautin, D.G., 1988. Anthozoan dominated benthic environments. *Proceedings of the 6th International Coral Reef Symposium*, **3**, 231–236.
- Fautin, D.G., 1991. The anemonefish symbiosis: what is known and what is not. *Symbiosis*, **10**, 23–46.
- Fautin, D.G. & Allen, G.R., 1997. *Field guide to anemonefishes and their host sea anemones*, 2nd edn. Perth, Australia: Western Australian Museum. Electronic version: <http://biodiversity.uno.edu/ebooks/intro.html>
- Fishelson, L., 1965. Observations and experiments on the Red Sea anemones and their symbiotic fish *Amphiprion bicinctus*. *Bulletin of the Sea Fisheries Research Station Haifa*, **39**, 1–14.
- Fishelson, L., 1970. Littoral fauna of the Red Sea: the population of non-scleractinian anthozoans of shallow waters of the Red Sea (Eilat). *Marine Biology*, **6**, 106–116.
- Fricke, H.W., 1974. Öko-Ethologie des monogamen Anemonenfisches *Amphiprion bicinctus*. *Zeitschrift für Tierpsychologie*, **36**, 429–512.
- Fricke, H.W., 1983. Social control of sex: field experiments with the anemonefish *Amphiprion bicinctus*. *Zeitschrift für Tierpsychologie*, **61**, 71–77.
- Hattori, A., 1991. Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. *Japanese Journal of Ichthyology*, **38**, 165–177.
- Holbrook, S.J. & Schmitt, R.J., 2005. Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemonefish. *Coral Reefs*, **24**, 67–73.
- Maroz, M. & Fishelson, L., 1997. Juvenile production of *Amphiprion bicinctus* (Pomacentridae, Teleostei) and rehabilitation of impoverished habitats. *Marine Ecology Progress Series*, **151**, 295–297.
- Mergner, H., 1971. Structure, ecology and zonation of Red Sea reefs (in comparison with South Indian and Jamaican reefs). *Symposium of the Zoological Society of London*, **28**, 141–161.
- Nagelkerken, I., Roberts, C.M., Velde, G. van der, Dorenbosch, M., Riel, M.C. van, Cocheret de la Morinière, E. & Nienhuis, P.H., 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series*, **244**, 299–305.
- Ochi, H., 1986. Growth of the anemonefish *Amphiprion clarkii* in temperate waters, with special reference to the influence of settling time on the growth of 0-year-olds. *Marine Biology*, **92**, 223–229.
- Porat, D. & Chadwick-Furman, N.E., 2004. Effects of anemonefish on giant sea anemones: expansion behavior, growth and survival. *Hydrobiologia*, **530/531**, 513–520.
- Porat, D. & Chadwick-Furman, N.E., 2005. Effects of anemonefish on giant sea anemones: ammonium uptake, zooxanthella content and tissue regeneration. *Marine and Freshwater Behaviour and Physiology*, **38**, 43–51.
- Richardson, D.L., 1999. Correlates of environmental variables with patterns in the distribution and abundance of two anemonefishes (Pomacentridae: *Amphiprion*) on an eastern Australian sub-tropical reef system. *Environmental Biology of Fishes*, **55**, 255–263.
- Sargent, R.C. & Wagenbach, G.E., 1975. Cleaning behavior of the shrimp, *Periclimenes antrophilus* Holthuis and Eibl-Eibesfeldt (Crustacea: Decopoda: Natantia). *Bulletin of Marine Science*, **25**, 466–472.
- Vago, R., Achituv, Y., Vaki, L., Dubinsky, Z. & Kizner, Z., 1998. Colony architecture of *Millepora dichotoma* Forsskål. *Journal of Experimental Marine Biology and Ecology*, **224**, 225–235.

Submitted 9 May 2005. Accepted 29 July 2005.